

Macroevolutionary interplay between planktic larvae and benthic predators

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ABSTRACT

Many marine invertebrates have a complex life cycle in which the egg develops into an intermediate planktic larval form rather than developing directly to the benthic juvenile stage. Because of the evolutionary and ecological complexity of pelagic-benthic life cycles, the reasons behind the origin of larvae and their subsequent maintenance over geological time are not well understood. Using both a molecular clock and the fossil record, I show that the initial exploitation of the predator-free pelagic realm by lecithotrophic larvae was achieved independently multiple times by the end of the Early Cambrian, and that the convergent evolution of planktotrophy from lecithotrophic ancestors evolved between the latest Cambrian and Middle Ordovician at least four, and possibly as many as eight, times. Both the exploitation of the pelagic realm by nonfeeding larvae and the acquisition of planktotrophy correlate in time with novel modes of benthic predation, including the dramatic rise in the number and type of epifaunal suspension feeders in the Early Ordovician.

Keywords: larvae, Cambrian, Ordovician, suspension feeding, predation.

INTRODUCTION

Approximately 70% of benthic marine species have a complex life cycle in which the egg, rather than developing directly into the benthic juvenile, develops instead into an intermediate larval form, many of which feed in the plankton before undergoing metamorphosis (Thorson, 1950). Pelagic-benthic life cycles are of sufficient ecological and evolutionary complexity that the reasons behind their origin and maintenance over geological time are not well understood (Strathmann, 1985, 1993; Pechnick, 1999). The usual suspect, dispersal, is vigorously debated; some argue that, despite its potential macroevolutionary importance (e.g., Hansen, 1978; Jablonski, 1986; Jeffery and Emlet, 2003), dispersal cannot explain the origin or maintenance of feeding larvae (Palmer and Strathmann, 1981). Pechenik (1999) argued that the maintenance of a feeding larval stage may have more to do with the difficulty in losing the larva than with some selective advantage provided to the animal. If true, then understanding the origins of larvae can only be achieved if the question is rooted within the environment in which they arose (Strathmann, 1993).

In their seminal paper on the evolving relationship between the plankton and the benthos, Signor and Vermeij (1994) argued that nonfeeding larvae arose during the Ediacaran, and feeding larvae arose during the Late Cambrian–Early Ordovician, triggered, in part, by the appearance of benthic predators, especially tiered suspension feeders. Here I show, using the molecular clock estimates of Peterson and Butterfield (2005), the phylogenetic logic of Strathmann (1978), and the fossil record, that Signor and Vermeij (1994) were broadly correct—nonfeeding larvae arose multiple times independently in the late Ediacaran, correlating with the first appearance of macroscopic trace fossils, and planktotrophy arose a number of times independently starting in the latest Cambrian, correlating with the dramatic rise in the number and types of benthic epifaunal suspension feeders.

DATING THE ORIGINS OF MARINE LARVAE

To determine when the various larval forms evolved, key divergence times of larval-bearing taxa were estimated using both a molecular clock and the fossil record. All molecular clock dates are from

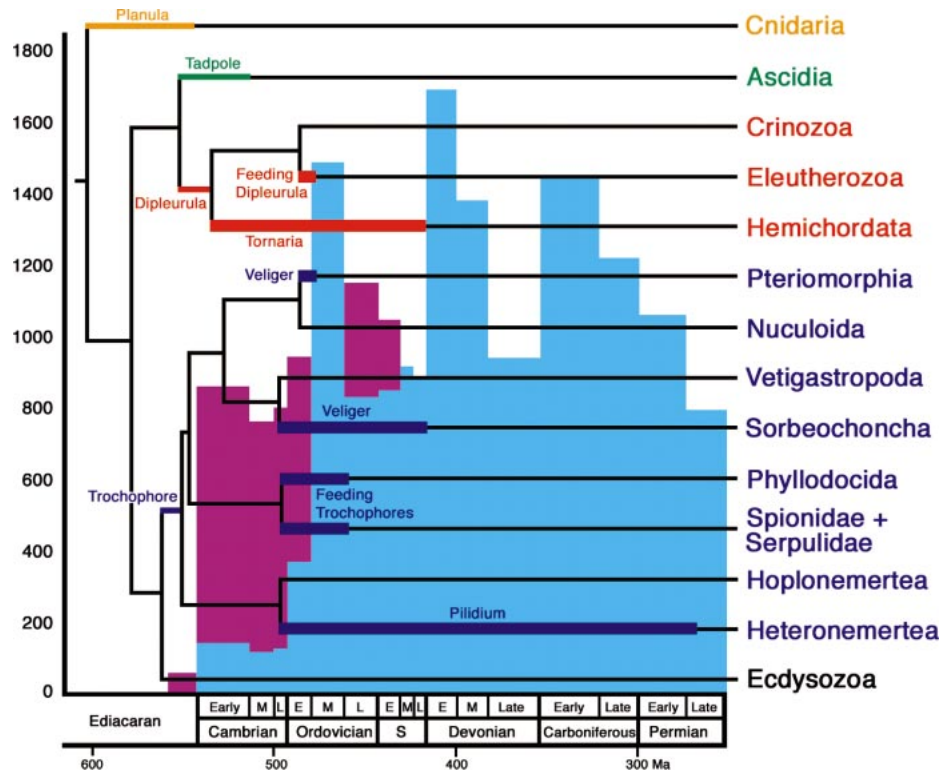
Peterson and Butterfield (2005), except where indicated. Deuterostomes have two very different larval types: echinoderms and hemichordates have a ciliated larval form, the dipleurula (Fig. 1, red); whereas ascidians have a nonciliated larval form, the tadpole (Fig. 1, green). Molluscs, annelids, and nemerteans are characterized by a third ciliated larval form, the trochophore (Fig. 1, blue). A fourth ciliated larval form, the planula, is only found in cnidarians (Fig. 1, orange). All four of these larval forms are presumed to be primitively epibenthic and nonfeeding (Haszprunar et al., 1995; see following), and evolved independently from one another (contra Peterson et al., 2000; see Peterson et al., 2005, for a recent perspective).

The minimum for the evolution of the dipleurula is 535 Ma, the divergence between echinoderms and hemichordates. The maximum, which was not dated by Peterson and Butterfield (2005), is the 550 Ma divergence between chordates and echinoderms (Aris-Brosou and Yang, 2002). This is also the maximum for the evolution of the tadpole larva. The minimum is the 520 Ma ascidian fossil from Chengjiang (Chen et al., 2003). This, of course, assumes that the larva is at least as ancient as the adult form, which is reasonable given that the adult is attached to trilobite debris, suggestive of an epibenthic stage during its development. With respect to the trochophore, because recent data suggest that the planuliform larva of paleonemerteans is a modified trochophore (Maslakova et al., 2004), the minimum is the 549 Ma divergence between nemerteans and annelids + molluscs. The maximum is the 561 Ma divergence between the trochozoans and the ecdysozoans. Finally, the evolution of the cnidarian planula is younger than 604 Ma, the estimated divergence between cnidarians and triploblasts, but older than 543 Ma, the estimated divergence between the anthozoan *Metridium* and the hydrozoan *Obelia*. This is the same geological window as the three triploblast larval forms discussed here, and thus, consistent with prediction (Signor and Vermeij, 1994), pelagic-benthic life cycles are of great antiquity, evolving at least four times independently during the late Ediacaran (Fig. 1).

EVOLUTION OF PLANKTOTROPHY

The geologically simultaneous rise of epibenthic larvae during the late Ediacaran is further evidence for a planktonic revolution at the

Figure 1. Origin of larval types as deduced from fossil record and molecular clock. Molecular clock suggests that three different larval forms, planula (orange), dipleurula (red), and trochophore (blue), all evolved during Ediacaran (thin colored lines). Fossil record also suggests that ascidian tadpole larva (green) evolved during this same time interval. Fossil record and molecular clock suggest that at least six different feeding larval forms evolved from nonfeeding ancestors sometime between Late Cambrian and end of Silurian (indicated by thick colored lines); only nemertean pilidium and bryozoan cyphonautes (not shown due to uncertainty concerning their phylogenetic position) could have evolved at a significantly younger date. Shown in light blue is generic fossil record (at 1 X; see scale on left) of five different epifaunal suspension feeding taxa: cnidarians, ectoprocts, brachiopods, benthic graptolites, and noneleutherozoan echinoderms (Sepkoski, 2002). Only these five were considered because, although other taxa have epifaunal suspension feeding species, clades like polychaete annelids and bivalve molluscs are too trophically diverse to easily tabulate the number of obligate epifaunal suspension-feeding genera. Of note is that dramatic rise in number and types of epifaunal suspension-feeding genera follows origin of four nonfeeding larval forms, but corresponds to evolution of planktotrophy in multiple lineages. Fossil record of ichnogenera (at 0.1 X) (modified from Crimes and Droser, 1992; S. Jensen, personal commun., 2005; M. Droser, personal commun., 2005.) is also shown (purple). Origin and dramatic rise in number of ichnogenera correlate with origin of nonfeeding larvae in late Ediacaran–Early Cambrian.



Proterozoic–Cambrian transition (Butterfield, 1997, 2001). Of interest, however, is that unequivocal evidence for planktotrophy is not evident until the Tommotian (Butterfield, 1997, 2001), and, given the nature of the evidence (the rapid appearance of antipredatory spines in planktic acritarchs), could not have evolved much earlier (Butterfield, 2003). It is likely, then, that lecithotrophy is primitive for most groups, consistent with both the fossil record (Chaffee and Lindberg, 1986) and several detailed phylogenetic studies that polarize the direction of evolutionary change (Fig. 2A). For example, the feeding larval form of nemerteans, the pilidium, is only found in heteronemerteans and in *Hubrechtella*, but not in the basal “paleonemerteans” or hoplonemerteans, which are characterized by the nonfeeding planuliform larva (Norenberg and Stricker, 2002). Within molluscs, aplousobranchs, polyplacophorans, scaphopods, and the basal clades within both gastropods and bivalves are characterized by lecithotrophic trochophores; feeding trochophores (i.e., veligers) are inferred to have evolved twice independently, once within Gastropoda and once within Bivalvia (Haszprunar et al., 1995).

To date the appearance of feeding larval forms, I used the molecular clock to estimate the divergence times between two polychaete annelids (*Chaetopterus* and *Nereis*), and between two heteronemerteans (*Lineus* and *Cerebratulus*) and the hoplonemertean *Amphiporus*. Phylogenetic considerations suggest that the last common ancestor of the polychaete annelids *Chaetopterus* and *Nereis* possessed a nonfeeding trochophore larval form (Rouse, 2000). The molecular clock estimates the divergence between these two polychaetes at 493 Ma (Fig. 1). Because close relatives with feeding larval forms of both *Chaetopterus* and *Nereis* are known from fossils dating to the Middle Ordovician (Wills, 1993), the minimum for the evolution of at least two polychaete feeding trochophores is ca. 460 Ma (Fig. 1). The molecular clock dates the divergence between the two heteronemerteans at 270 Ma, and the divergence between the hoplonemertean *Amphiporus* and the two heteronemerteans at 485 Ma (Fig. 1).

These data suggest that the maximum for the evolution of annelid feeding larval forms and the nemertean pilidium is latest Cambrian–Early Ordovician. This happens to coincide with the maximal age for several other feeding larval forms, including the bivalve and gastropod veligers, and the bryozoan cyphonautes (Taylor, 1993; Signor and Vermeij, 1994). It may also coincide with the maximal age of the echinoderm feeding larval form, assuming that the absence of a feeding larval stage in pelmatozoan echinoderms and pterobranch hemichordates is primitive. The molecular clock and the fossil record indicate that at least six of the eight feeding larval forms considered here had all evolved by the beginning of the Devonian (and four of these by the Middle Ordovician); only the pilidium and the cyphonautes (Taylor, 1993) could have evolved substantially later. Therefore, at least four, and possibly as many as eight, different feeding larval forms had evolved independently from nonfeeding ancestors between the Late Cambrian and the Middle Ordovician (Fig. 1).

A significant difference between the Cambrian and Ordovician is that the Cambrian benthos contained relatively few suspension feeders with the capacity to feed upon eukaryotic plankton. Instead, the Cambrian suspension-feeding fauna was dominated by sponges, a group of animals that by physiological necessity feed primarily on organic detritus and demersal bacteria (discussed in Peterson et al., 2005). It was not until the Early Ordovician that tiered suspension-feeding communities with the capacity to feed upon metazoan larvae begin to compose a significant fraction of the benthic suspension-feeding fauna (Signor and Vermeij, 1994). This dramatic rise in generic diversity (Fig. 1, light blue) correlates with the evolution of planktotrophy in at least four, if not eight, of the eight clades discussed herein.

DISCUSSION

These data and observations are consistent with the hypotheses of Signor and Vermeij (1994), i.e., that the multiple origins of feeding larvae were a two-step process. The initial exploitation of the pelagic

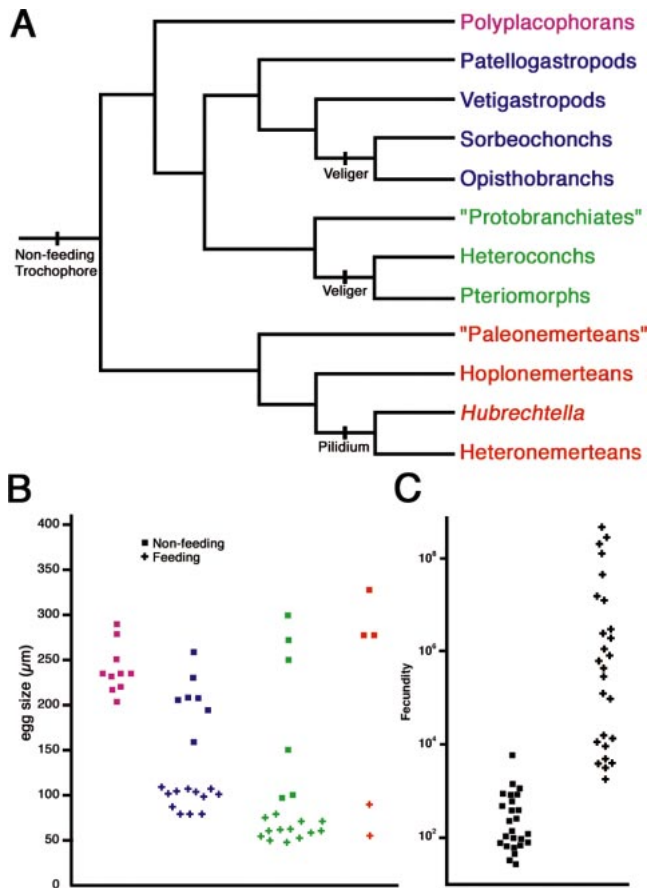


Figure 2. Derived nature of planktotrophy within molluscs and nemerteans and its relationship to egg size and fecundity. **A:** Phylogenetic tree showing presence of lecithotrophy in basal taxa of both molluscs and nemerteans. Note that both “protobranchiates” and “paleonemerteans” are paraphyletic (indicated with quotes), and thus there are multiple lineages of lecithotrophs at base of both Bivalvia and Nemertea. Three feeding larval forms each evolved once independently: veliger forms in bivalves and gastropods, and pilidium in *Hubrechtella* and heteronemerteans. Phylogeny from Giribet and Wheeler (2002), Thollessen and Norenburg (2003), and Lindberg and Guralnick (2003). **B:** Relationship between planktotrophy and egg size in molluscs and nemerteans. Feeding taxa are indicated with cross, and nonfeeding with square, color coded to match higher taxon name in A. Data from Costello et al. (1957) and Strathmann (1987). **C:** Relationship between fecundity and feeding type. Planktotrophs produce order of magnitude more eggs per female as compared with lecithotrophs (modified from Thorson, 1950). Note that these trends are not restricted to molluscs and nemerteans, but reflect general considerations across a wide variety of taxa (e.g., see Emlet et al. [1987] for data on echinoderms).

realm by nonfeeding larvae was achieved independently multiple times by the end of the Early Cambrian, and was most likely driven by benthic predation pressures on eggs and developing embryos (see also Butterfield, 1997, 2001, 2003; Peterson et al., 2005). Trace fossils clearly show the origins of macroscopic bilaterian grazers by the late Ediacaran, ca. 555 Ma (Martin et al., 2000) (Fig. 1, purple), with an explosion of forms into the Early Cambrian (Crimes and Droser, 1992). Unlike the benthos, the pelagic realm was free of predators until the latest Early Cambrian (Peterson et al., 2005), and thus the initial exploitation of the pelagic realm was initially achieved without any influence from epibenthic predation.

Once epibenthic predation is established, it is often thought to be the principal factor governing subsequent larval evolution (Thorson,

1950). Nevertheless, recent studies suggest that larvae experience very little predation while in the pelagic realm (Johnson and Shanks, 2003). Clearly, epibenthic predation occurs, as some larval forms possess structures designed to interfere with pelagic (but not benthic, Cowden et al., 1984) predation (e.g., Hickman, 2001; Nützel and Fryda, 2003). However, the molecular clock and the fossil record (Fig. 1) clearly show that despite the presence of epibenthic predators (Peterson et al., 2005), larvae increased the amount of time they spent in the plankton. Thus, although spending a longer amount of time in the plankton will increase the chances of encountering a pelagic predator, epibenthic predation does not appear to be a strong selective force in the evolution of complex life cycles.

Rather than driven by planktic predation, the evolution of planktotrophy instead was possibly driven by benthic predation. The correlation between the multiple and independent experiments in the evolution of planktotrophy, and the dramatic rise in the number and types of epifaunal suspension feeders, may be causal (Signor and Vermeij 1994). The hypothesis presented here is that suspension feeding selected for fecundity, resulting in selection of planktotrophy (see also Palmer and Strathmann, 1981). As is well known (e.g., Thorson, 1950), a reduction in egg size, compared to lecithotrophs, is associated with planktotrophy, which allows for a dramatic increase in absolute egg number (fecundity) (Figs. 2B, 2C) but demands that the larva feed in order to become competent to undergo metamorphosis. Thus, suspension feeders could exert a selection pressure to evolve planktotrophy because the antipredatory strategy is to simply overwhelm them by egg numbers. Planktotrophy is, in theory, quite simple to evolve, given that it requires only an animal of the appropriate mass (Olive, 1985; Chaffee and Lindberg, 1986), and a relatively trivial shift in the developmental timing of the gut. Thus, contrary to Thorson’s (1950) original hypothesis, larval wastage is not an adaptation to counter planktic mortality, but instead to counter mortality upon settlement.

Benthic predation may also drive the multiple reversals back to lecithotrophy. Since the Ordovician, there have been numerous and independent losses of feeding larva, but few secondary gains (Strathmann, 1978), suggesting that, after the Ordovician, lecithotrophy has had a higher fitness than planktotrophy. One possible reason is that adaptations that protect early embryonic stages from benthic predators are associated with the secondary evolution of lecithotrophy. For example, planktotrophic eggs are negatively buoyant, and thus ripe for predation as they sink to the benthos. However, in many eleutherozoan echinoderms the loss of the feeding larval form is correlated with the acquisition of a larger, positively buoyant, egg (Emlet et al., 1987; Emlet, 1994). Thus, although the loss of planktotrophy results in decreased fecundity, there is also the potential decrease in egg mortality, given that it does not encounter the benthos until it has developed into a juvenile. Several other taxa have evolved unique solutions to counter negative buoyancy, including crinoids (Holland, 1977), chitons (Buckland-Nicks, 1993), and ascidians (Lambert and Lambert, 1978); still other taxa brood or encapsulate their eggs and embryos to protect them from predators (Pechenik, 1979).

The secondary evolution of lecithotrophy and the increase in egg size reduce the mortality of the early embryo (due to positive buoyancy and other protective devices), the larva (due to decreased time spent in the plankton), and the juvenile (due to an increase in absolute size and the potential to rely on stored nutrients during the early juvenile period) (Emlet and Houegh-Guldberg, 1997; Levitan, 2000), all of which offset the cost of reduced fecundity and increase fitness (Havenhand, 1993). Therefore, the origins of feeding larvae are a strategy against a unique set of evolutionary and ecological circumstances that arose in the Early Ordovician, but alternative strategies of greater selective advantage were discovered later in geologic time by many taxa independently.

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